THE ARRIVAL PATTERN OF TRICHOPTERA AT ARTIFICIAL LIGHT NEAR MONTREAL, QUEBEC *

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The arrival pattern of Trichoptera at artificial light at Ile Ste. Hélène, in the St. Lawrence River opposite Montreal, Quebec, is examined. A Robinson trap with a mercury vapour light bulb was combined with a Lafrance trap which changed containers hourly. Ten minute catch periods were used to examine the evening peak in detail, containers being changed manually. Numbers and sex ratios for each of 78 species taken are given. One species not then described, and two other doubtful forms, females, were noted. Thirty one genera and thirteen families are represented. The pattern in each of 7 species examined in detail is nocturnally bimodal, with only a small morning peak. The roles of light, temperature, wind, relative humidity, and saturation deficit in determining total catches per night and fluctuations of numbers within any one night, are examined. Temperature and wind are the primary factors, with light fixing the time of the evening and morning peaks. Neither relative humidity nor saturation deficit seemed to be of any significance, at the values experienced. A differential effect of wind on flight, depending on species size, is shown. Sex ratios throughout the night are briefly examined, and it is concluded that no one sex of any of the seven major species is alone responsible for any peak. It is considered that the pattern of arrival at light reflects a natural pattern of flight activity.

It has previously been found that in East Africa (Corbet & Tjønneland 1955) the numbers of Trichoptera at lights vary throughout the night according to a pattern. This study is an investigation of the arrival pattern of Trichoptera at artificial light at night at Ile Ste. Hélène in the St. Lawrence River opposite Montreal, Quebec. The effects of meteorological factors, including natural light, on the pattern were examined. While the study deals with the pattern of arrival at artificial light, and the results can only be directly interpreted within the observed conditions, some attempt is made in the discussion to relate the pattern found to the natural pattern of flight activity, independent of artificial stimuli.

METHODS AND EQUIPMENT

To examine patterns of animal activity relative to time, the time involved must be subdivided to a number of equal periods, here called 'catch periods' or just 'periods'. The population at light was sampled during successive catch periods. To compare patterns between nights and obtain meaningful average patterns for the summer, it is necessary to start any one chosen catch period at the same solar time each evening.

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Two solar times were used: sunset (solar elevation minus 0.83°) and civil twilight (solar elevation minus 6°). These times, translated to local clock time for each night, were obtained from tables prepared by the Dominion Observatory, Ottawa, and the Meteorology Branch of the Canada Department of Agriculture, Ottawa. The times were prepared for the latitude and longitude of Ile Ste. Hélène (45°31'N, 73°32'W).

It was decided to examine the pattern of the entire night using 1 hr catch periods, the first of which was to start one half hour prior to sunset, and to examine the evening peak in more detail, using 10 minute periods, starting one hour prior to civil twilight. Civil twilight was used for the 10 min catches as it was noted after running several nights at 1 hr periods that the massive upsurge to the evening peak generally occurred in the second period, in which civil twilight also occurred. It was felt that civil twilight might be of significance to the evening peak of flight activity and the 10 min sessions were designed to determine the timing and form of the evening peak, and perhaps the factors controlling it.

The 1 hr catching period nights always ran for a total of 12 hrs as this was the capacity of the automatic trap used and covered the entire night, ending well past sunrise. As many as 19 ten minute periods were run on some nights, but 13 was decided on as the minimum which sufficed to cover the period of peak flight activity. On one night trapping was stopped after 9 periods due to cold; the data are only used in the results when considering catch nights individually.

Trapping Methods and Equipment

Trapping was done at the old Fort (figs. 1 & 2). The 1 hr catches were taken with a mechanical trapping device designed and built by Mr. J. Lafrance (1965) of the Canada Department of Agriculture Laboratory, St. Jean, Quebec, and loaned for this study. It is capable of hourly (± 2 min) changing of catch canisters, but can be adjusted for other periods. Capacity is 12 canisters, and the killing agent used was 70% ethanol.

The insects reached the cans by way of a large funnel on top of the trap body, with the spout passing through the roof to the cans below. On top of the funnel was placed the metal cone of a Robinson trap (Robinson & Robinson 1950), which bears a socket for an 'Osram' 125 watt, high pressure mercury vapour light bulb (230-240 volts; model MB/V). The light from this bulb is particularly rich in UV light, and is highly attractive to Trichoptera in consequence (Williams 1951). The spectral composition of light from a similar source is given in table 1. A cylindrical collar, 7" high by 13" diameter, made of file-folder card was placed around the upper edge of the Robinson cone to reduce the intensity after an abortive first use of the trap in which so many Trichoptera arrived as to swamp the cans and necessitate rejection of the catches for that night. It was used for both 1 hr and 10 min catches. Even so, some of the catches taken on some nights were beyond the capacity of the machine. When this was so the entire night's catches were discarded. Intrinsic to the Robinson trap cone are 4 vanes set at 90° to each other on the inner surface, which serve to stun the insects as they spiral inwards and downwards towards the light; they then fall into the ethanol below. The vanes also served to hold the collar in place and hold the light bulb socket. This part of the Robinson trap was retained and temporarily coupled to the Lafrance trap.

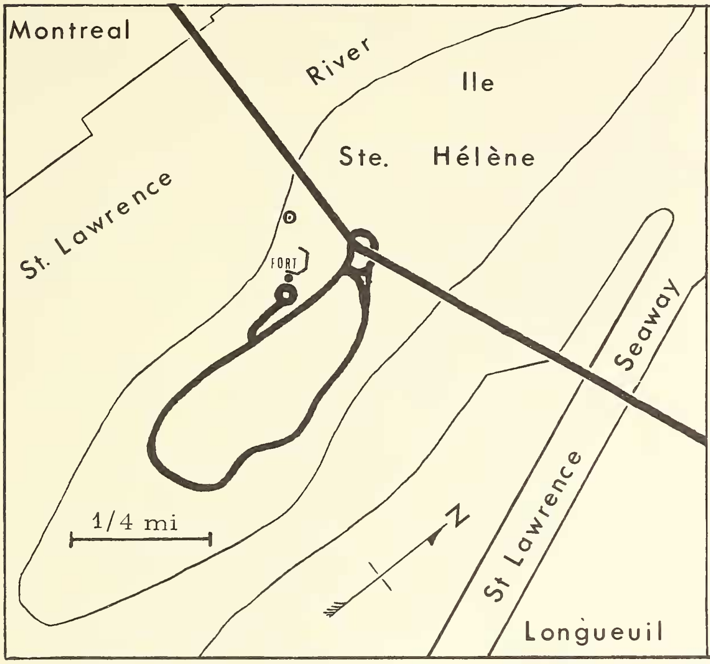

Figure 1

ILE STE. HÉLĒNE

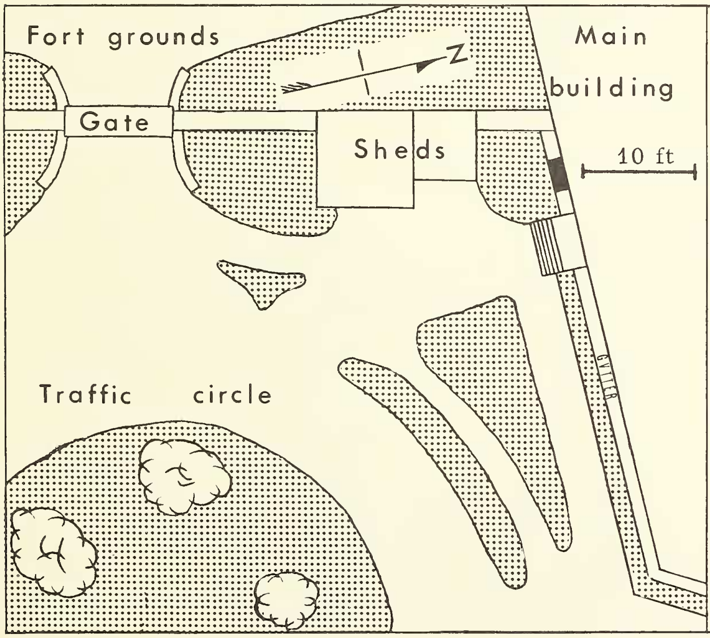

Figure 2

LIGHT TRAP LOCATION

TABLE 1 - Intensity of the radiation from a high pressure mercury vapour bulb corrected for transmission through lime - soda glass (from Rössler 1939).

Wavelength (Å)	5791	5770 -5791	5461	4916	4358	4047*	3906
Relative energy in watts	6.39	4.99	6.10	.063	4.90	3.23	.054
Wavelength (Å)	3650	3341	3126	3022	2967	2925	2894
Relative energy in watts	6.62	.374	1.51	.215	.046	.002	.004

* Lower limit of visible radiation in this spectrum.

The same equipment was used to take the 10 minute catches except that as the Lafrance trap could not be set for ten minute intervals, the jar was changed manually every ten minutes. Other conditions were as identical as possible to those of the 1 hr catch periods. The nights on which trapping took place, and other relevant data, are set out in table 2 (1 hr catches) and table 3 (10 min catches).

TABLE 2 - Dates and times (eastern daylight saving) of the first of 12 consecutive 1 hr catches of Trichoptera at Ile Ste. Hélène Montreal, summer 1964.

Date	Correct sunset time	Start of first period (p.m.)	Error (mins)
13-14 June	8.45	8.15	0
16-17 "	8.45	8.15	0
17-18 "	8.45	8.15	0
27-28 "	8.48	8.18	0
1 - 2 July	8.47	8.17	0
4 - 5 "	8.46	8.16	0
6 - 7 "	8.45	8.16	+ 1
13-14 "	8.41	8.12	+ 1
18-19 "	8.38	8.09	+ 1
23-24 "	8.33	8.04	+ 1
1 - 2 August	8.22	7.54	+ 2
3 - 4 "	8.19	7.52	+ 3
8 - 9 "	8.13	7.45	+ 2
12-13 "	8.06	7.39	+ 3
19-20 " *	7.55	7.25	0
25-26 "	7.44	7.14	0

* Catch 12 not obtained.

TABLE 3 - Dates and times (eastern daylight saving) of the first of series of 10 minute catches of Trichoptera, at Ile Ste. Hélène, Montreal, summer 1964.

Date	Start (p. m.)* of first catch	Number of catches	End of last catch
2 - 3 July	8.24	19	11.34
7 - 8 "	8.23	16	11.03
14-15 "	8.18	18	11.18
19-20 "	8.14	14	10.34
24-25 "	8.09	18	11.09
6 - 7 August	7.51	13	10.01
13-14 "	7.50	9	9.20
23-24 "	7.22	13	9.23
26-27 "	7.17	13	9.27
30-31 "	7.09	13	9.19

* One hour prior to civil twilight.

Other Observations

All the 1 hr catches were taken in the period for which continuous records of temperature, relative humidity, wind, and rainfall were made on the island, except that wind recording started after the first trapping night, June 13. The records used here are from the West Station (see fig. 1), about 20 ft horizontally from the edge of the river, but about 50 ft above the water and 1/4 mile from the trapping site. The station was set up and maintained by the Canada Department of Transport, in conjunction with the Shadfly Project.

Temperature and relative humidity were read from the charts obtained at the mid-point of each 1 hr catch period; wind speed, in miles per hour, is averaged for each catch period; saturation deficit was obtained from temperature and relative humidity by tables. Zenith light intensity readings were taken at the mid-point of each 10 min period. It was later discovered that the light readings could not be converted to foot-candles as the precise spectral sensitivity of the sensor unit was unknown and could not easily be determined. It has been possible, however, to obtain a curve of light intensity in arbitrary units (p. 238). As time permitted, notes on cloud, rainfall, and wind were taken.

Treatment of Catches and Data

Generally, all Trichoptera taken were determined to species and sex. Without exception all were counted. But occasionally a species or group of species, Hydroptilidae especially but also Hydropsychidae and *Protoptila maculata* (Hagen), were taken in such numbers that the proportions of each species and sex had to be estimated from a sub-sample. Selection of sample size was arbitrary but in general the larger the total numbers, the smaller the per cent sampled.

To reduce the effect of fluctuations due to environmental factors, the arithmetic values (n) may be transformed to the logarithmic value (log n). To bypass the difficulty of zeros, for which there is no logarithmic value, Williams (1937) suggested adding one (1) to all values in a time series, and transforming the resulting values (n + 1) to logarithms. If the log (n + 1) values for all periods of any one time series, or equivalent periods in terms of solar time of several time series are averaged, $[\Sigma \log (n + 1)] / N$ and the antilog taken, an approximation to the geometric mean of the series is obtained. This approximation is known as Williams' mean (Haddow 1960), and is symbolized as M_W. The value $\Sigma \log (n + 1) / N$, when obtained for equivalent periods of several time series and plotted against time gives an average pattern for these time series.

RESULTS

Numbers of Specimens Examined

Table 4 lists the species taken, in descending order of numbers taken per species in all catches. The total number of specimens of Trichoptera was 297, 967 for all species. A total of 78 species, in 31 genera and 13 families was taken, plus 2 doubtful forms. One of these, *Cheumatopsyche montrealensis* Nimmo (1966) was not then described. The following species were selected for detailed examination of data, and are given in order of abundance: *Hydroptila spatulata* Morton, *Cheumatopsyche speciosa* (Banks), *Protoptila maculata* (Hagen), *Hydropsyche recurvata* Banks, *Psychomyia flavida* Hagen, *Athripsodes cancellatus* (Betten), and *Athripsodes tarsipunctatus* (Vorhies). *Agraylea multipunctata* Curtis was not selected although more numerous than *Athripsodes tarsipunctatus* because the catch was spread over 27 nights whereas that of *A. tarsipunctatus* was concentrated into 18. Also in table 4, the total numbers per species are broken down to sexes, sex ratios (per cent males) as in Henderson, Henderson & Kenneth (1960), and finally the range of dates on which each species was taken is given, concerning which it must be remembered that trapping started on June 2 and ended August 31.

The ratios may be artifacts of the trapping method, due to differential attraction of the sexes. One remarkable fact emerges from table 4, however. *P. flavida* shows a sex ratio of virtually zero. Marshall (1939) obtained similar results, but cautioned about the possible differential attraction. Betten (1934) states that he had only 2 specimens, females, but that Sibley (1926) took 893, in an unspecified manner, all of them female. If this is the natural ratio, then *P. flavida* must be usually parthenogenetic. Crichton (1960) considers in detail only the ratios of species with over 100 individuals taken, which is also done here. Only 26 species qualify of which 17 give ratios above 50, 3 of them close to this: *Leptocella candida* (52. 00), *Agraylea multipunctata* (53. 05) and *Athripsodes ancylus* (53. 78).

Pattern of Arrival at Artificial Light

The data will be examined first in the form of total numbers of Trichoptera per catch, after which the separate data on the previously selected species will be examined, for both 1 hr and 10 min catches.

TABLE 4 - Species of Trichoptera taken at Ile Ste. Hélène, Montreal, summer 1964 in descending order of numbers taken in both 1 hr and 10 min catches.

Species	Total	♂♂	Sex ratio (%♂)	Range of dates when taken
Hydroptila spatulata Morton	114,980	94,220	81.94	13 Jun. -30 Aug.
Cheumatopsyche speciosa (Banks)	54,582	25,616	46.93	13 Jun. -30 Aug.
Protoptila maculata (Hagen)	50,738	30,323	59.76	19 Jun. -30 Aug.
Hydropsyche recurvata Banks	32,515	18,190	56.82	2 Jun. -30 Aug.
Psychomyia flavida Hagen	13,015	2	0.02	13 Jun. -30 Aug.
Athripsodes cancellatus (Betten)	9,951	7,766	78.04	1 Jul. -26 Aug.
Agraylea multipunctata Curtis	5,229	2,773	53.05	3 Jun. -30 Aug.
Athripsodes tarsipunctatus (Vorh.)	4,107	2,985	72.68	27 Jun. -25 Aug.
Cheumatopsyche campyla Ross	2,598	716	27.56	2 Jun. -30 Aug.
Hydroptila waskesia Ross	1,598	1,466	91.74	1 Jul. -20 Aug.
Hydroptila waubesiana Betten	1,182	817	69.12	13 Jun. -30 Aug.
Glossosoma lividum (Hagen)	897	541	60.30	2 Jun. -30 Aug.
Oecetis inconspicua (Walker)	695	276	39.70	16 Jun. -30 Aug.
Athripsodes annulicornis (Steph.)	674	231	34.27	2 Jun. - 5 Jul.
Cheumatopsyche sordida (Hagen)	610	185	30.30	27 Jun. -30 Aug.
Hydropsyche morosa Hagen	600	498	83.00	2 Jul. -30 Aug.
Hydropsyche scalaris Hagen	593	294	49.60	4 Jul. -30 Aug.
Hydroptila perdita Morton	577	530	91.80	14 Jun. -30 Aug.
Hydropsyche bifida Banks	440	237	53.80	13 Jun. -25 Aug.
Polycentropus cinereus Hagen	428	311	72.60	14 Jun. -30 Aug.
Neureclipsis crepuscularis (Walker)	341	247	72.40	14 Jun. -30 Aug.
Leptocella candida (Hagen)	325	168	52.00	27 Jul. -30 Aug.
Brachycentrus lateralis (Say)	184	80	43.40	2 Jun. -14 Jun.
Hydropsyche placoda Ross	146	107	73.20	13 Jun. -26 Aug.
Oecetis immobilis (Hagen)	121	31	25.60	1 Jul. -30 Aug.
Athripsodes ancylus (Vorhies)	106	57	53.70	27 Jun. - 1 Aug.
Chimarra socia Hagen	96	59		19 Jun. -30 Aug.
Macronemum zebratum (Hagen)	92	59		27 Jun. - 1 Aug.
Athripsodes angustus (Banks)	63	23		14 Jul. - 8 Aug.
Mystacides sepulchralis (Walker)	59	36		27 Jun. -30 Aug.
Helicopsyche borealis (Hagen)	50	45		27 Jun. - 3 Aug.
Nyctiophylax vestitus (Hagen)	41	28		28 Jun. -19 Aug.
Oecetis cinerascens (Hagen)	41	24		2 Jul. -30 Aug.
Leptocella albida (Walker)	39	24		2 Jul. -25 Aug.
Hydropsyche walkeri Betten & Mosely	37	27		28 Jun. - 1 Aug.
Hydropsyche bronta Ross	19	12		19 Jun. -30 Aug.
Athripsodes punctatus (Banks)	19	8		13 Jul. - 1 Aug.
Hydroptila albicornis Hagen	17	16		13 Jul;6,30 Aug.
Athripsodes resurgens (Walker)	14	12		13 Jun. -19 Jul.
Athripsodes submacula (Walker)	14	10		13 Jun. -19 Jul.
Triaenodes flavescens Banks	14	1		13 Jul. -30 Aug.

TABLE 4 (cont.)

Species	Total	♂♂	Sex ratio (%♂)	Range of dates when taken
Triaenodes injusta (Hagen)	12	3		1 Jul. - 7 Jul.
Chimarra obscura (Walker)	9	7		1 Jul. -19 Jul.
Oecetis avara (Banks)	8	6		6 Jul. - 3 Aug.
Leptocerus americanus (Banks)	7	1		2 Jul. -14 Jul.
Athripsodes alagmus Ross	6	6		1 & 3 Aug.
Chematopsyche analis (Banks)	6	2		27 Jun. & 1 Aug.
Hydroptila hamata Morton	6	4		2, 14 Jul., 6 Aug.
Trianodes marginata Sibley	6	3		27 Jun. -30 Aug.
Oecetis osteni Milne	5	1		13 Jul., 26, 30 Aug.
Athripsodes dilutus (Hagen)	4	2		2 Jun. - 5 Jul.
Limnephilus moestus Banks	4	2		14 Jun. & 2 Jul.
Molanna musetta Betten	4	3		5 Jul.
Neotrichia okopa Ross	4	2		7 &19 Jul.
Athripsodes uvalo Ross	3	2		24 Jul.& 25 Aug.
Cheumatopsyche montrealensis Nimmo	3	3		27 Jun.
Molanna sp.	3	0		2 & 13 Jul.
Banksiola selina Betten	2	0		14 Jun. &2 Jul.
Hydropsyche sp.	2	0		13 Jun. &8 Aug.
Lepidostoma togatum (Hagen)	2	0		17 Jun. &2 Jul.
Limnephilus ornatus Banks	2	0		28 Jun. &5 Jul.
Limnephilus submonilifer Walker	2	0		17, 28 Jun., 2 Jul.
Neureclipsis validus (Walker)	2	0		2 & 5 Jul.
Phylocentropus placidus (Banks)	2	0		7 Jul. & 12 Aug.
Agapetus hessi Leonard & Leonard	1	0		27 Jun.
Anabolia ozburni (Milne)	1	0		2 Jul.
Cernotina sp.	1	0		19 Jul.
Hydropsyche vexa Ross	1	0		14 Jun.
Hydroptila armata Ross	1	0		19 Jul.
Hydroptila consimilis Morton	1	0		6 Aug.
Hydroptila virgata Ross	1	0		7 Jul.
Hydroptila sp.	1	0		13 Jul.
Leptocalla exquisita (Walker)	1	0		19 Aug.
Limnephilus hyalinus Hagen	1	0		2 Jul.
Neureclipsis bimaculatus (L.)	1	0		7 Jul.
Polycentropus nascotius Ross	1	1		5 Jul.
Rhyacophila melita Ross	1	1		14 Jun.
Setodes oligia (Ross)	1	0		7 Jul.
Triaenodes dipsia Ross	1	1		1 Jul.
Triaenodes tarda Milne	1	0		3 Jul.

Grand total 297,967

Species patterns follow closely the total numbers patterns. The average pattern for each species for the summer, will, however, be presented. Only 1 hr catches will be considered relative to weather, as it is impossible to read values accurately from the meteorological charts for intervals as small as 10 minutes.

1 Hour Catches - Total Numbers per Catch

In fig. 3 a peak occurs generally in the second period. In 2 of 15 nights the peak occurred in period three. This may be due to extrinsic factors obscuring or delaying the peak. A second peak, slight or otherwise, is found in the first or second period immediately prior to sunrise. This is the morning peak.

Between the two peaks, evening and morning, it is seen that adults are taken, occasionally in very nicely decreasing series, as in fig. 3(25-26 August), but often in widely varying numbers.

The average pattern for the summer, as determined by the nights on which trapping was carried out, is shown by fig. 4 (total numbers). The distinct evening peak is seen, but the morning peak is not manifest. This is due to sunrise shift during the season in relation to sunset and hence also in relation to the catch periods.

It remains now to demonstrate the dependence of the peaks on natural light intensity, and to explain the intervening period of gradual decline, or fluctuation as the case may be.

Dependence of the Peaks on Natural Light Intensity

The least fluctuating nightly graphs are selected for visual examination of the concomitant environmental factors. These graphs of fig. 3 (17-18 June, 13-14 July, and 25-26 August) show the peaks well. Table 5 presents the meteorological data for these three nights and examination shows that temperature is either declining throughout the night, usually slowly, or holding steady, but never increasing. Next, wind holds steady for at least the first two periods, in which the evening peak occurs. Finally, relative humidity and saturation deficit seem to fluctuate erratically. On the night of 13-14 July, however, they held steady for 5 hours preceding and including the morning peak. This seems to rule out these two factors as influencing the peak, at least at the values encountered here.

Thus meteorological factors are either declining fairly evenly, holding steady, or fluctuating and showing no correlation with log (n + 1), yet the peaks occur outstandingly. The first catch is fixed on time of sunset, and the evening peak always occurs in the same period, the second. The morning peak may occur in period 9, 10, or 11, depending on the season, but always in the pre-sunrise period.

Table 5 omits only light intensity. In the evening, with all factors generally declining, there is a peak in numbers of Trichoptera caught. In the morning, the same conditions prevailing, there is another peak in numbers caught. The only factor which has equal values in both evening and morning is light intensity. Obviously from the graphs, the light values involved occur after sunset and before sunrise. Thus the causal (or triggering) factor of both peaks appears to be a certain light intensity.

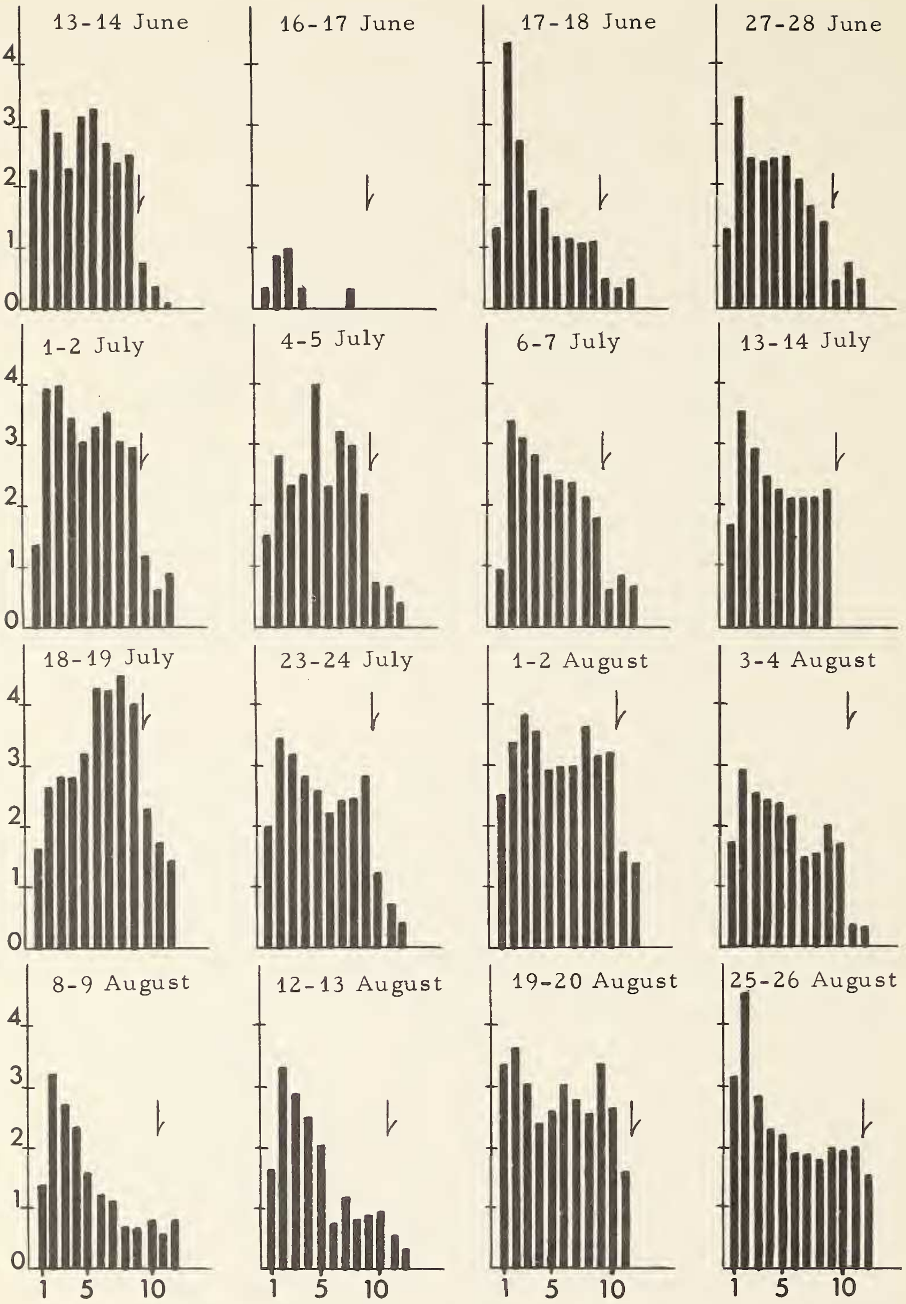

Figure 3 - Total hourly numbers of Trichoptera at UV light, Ile Ste. Hélène, Montreal, summer 1964. Abscissae 1 hr periods, ordinates log (n + 1), plotted at the period mid-points: Sunset coincident with first period mid-point. Arrows indicate approximate sunrise.

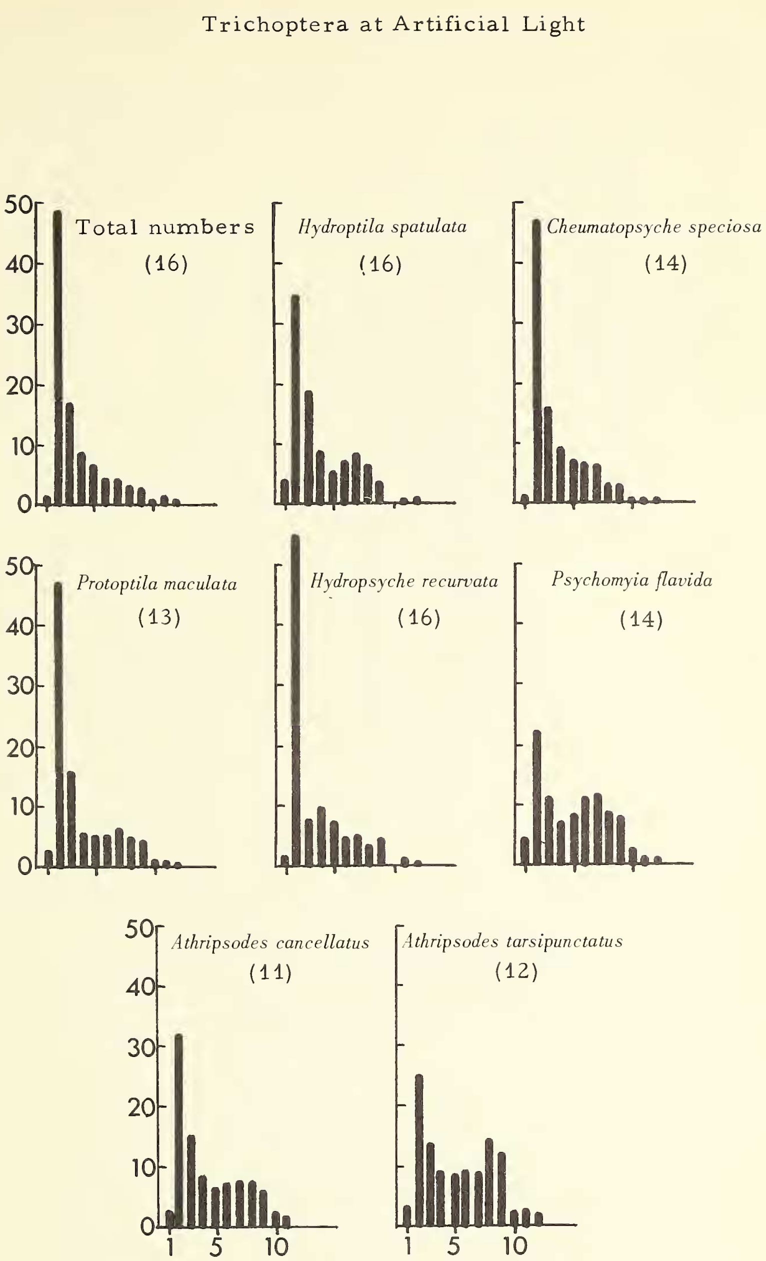

Figure 4 - Total numbers and numbers of 7 species of Trichoptera separately, taken at Ile Ste. Hélène, Montreal, in a UV light trap on 16 nights (or fewer), 1964; average values per 1 hr period for the summer. Abscissae 1 hr periods, ordinates Williams' mean (M_W) transformed to %. Sunset coincident with the first period mid-point.

TABLE 5 - Meteorological data and log (n + 1) of total numbers of Trichoptera taken per 1 hr period at Ile Ste. Hélène, Montreal, on three selected evenings, summer 1964.

	Period	log (n + 1)	T°F	Wind mph	% R.H.	* S.D.
June 17-18	1	1.30	63.5	6	29	0.42
	2	4.40**	63.0	7	32	0.39
	3	2.79	62.0	7	36	0.36
	4	1.89	61.0	7	39	0.33
	5	1.65	60.0	9	42	0.30
	6	1.18	60.0	8	46	0.28
	7	1.14	60.0	8	47	0.27
	8	1.04	59.0	10	49	0.25
	9	1.11**	60.0	9	50	0.26
	10	0.48	63.0	6	53	0.27
	11	0.30	63.0	7	57	0.25
July 13-14	1	1.62	71.0	2	85	0.11
	2	3.51**	70.0	1	82	0.12
	3	2.89	69.5	3	81	0.14
	4	2.42	69.5	3	84	0.12
	5	2.25	69.0	2	89	0.08
	6	2.09	68.5	2	88	0.08
	7	2.09	68.0	2	88	0.08
	8	2.08	68.0	2	88	0.08
	9	2.21**	68.0	1	88	0.08
	10	0	68.5	2	86	0.09
	11	0	69.0	1	84	0.10
August 25-26	1	3.14	73.0	9	58	0.34
	2	4.45**	69.0	9	60	0.28
	3	2.76	67.0	19	54	0.30
	4	2.21	67.0	19	70	0.20
	5	2.15	67.0	18	76	0.16
	6	1.81	67.0	15	79	0.14
	7	1.77	67.0	14	79	0.14
	8	1.74	66.0	15	76	0.15
	9	1.91	65.0	14	71	0.18
	10	1.85	64.0	14	72	0.17
	11	1.98**	63.0	13	72	0.17

* S.D. = saturation deficit, in inches of mercury.
** Peaks.

Effects of Other Environmental Factors

The night as a whole - Examined here are those periods of each night between and including sunset and sunrise.

Means of each factor, temperature, wind speed, relative humidity, and saturation deficit were obtained for each night. Each factor was then plotted against the mean log (n + 1) values for each night. As seen in fig. 5, temperature and log (n + 1) are clearly correlated; no other factor showed any significant correlation. That is, on an evening of high temperatures (70-80°F) one can expect a large catch, the opposite also holding true. Correlation coefficients are not calculated here as this is preliminary to an analysis of the data for the periods without sunlight. It should be noted that catches may be low despite high temperatures, due to relative seasonal scarcity of Trichoptera. This explains some lack of correlation in fig. 5. Other unrecorded or unrecognized factors may also be involved. Wind speed shows little apparent correlation with log (n + 1), although it can have a distinct effect on flight activity. The best available example is the night of 18-19 July (table 6):

TABLE 6 - Total numbers of Trichoptera taken, and meteorological data for 1 hr catch periods 1-9, 18-19 July, Ile Ste. Hélène, Montreal.

Catch period -	1	2	3	4	5	6	7	8	9
Log (n + 1)	1.60	2.57	2.73	2.71	3.15	4.20	4.15	4.40	3.91
T°F	89	88	87	86	85	85	84	83	83
Wind speed (mph)	24	25	25	23	14	8	5	3	1

Temperature was high and decreasing slowly. While a morning peak is clear, the evening peak is represented only by the small stubs in periods 2 and 3. As the wind dropped, rather abruptly, there was an upsurge in numbers of Trichoptera taken. This catch is one of the most useful of all catches taken. It will be noted that in fig. 5 the plotted position of 18-19 July is one of the poorly correlated catches. If the evening had been 'normal', wind being low or absent, the point would probably have been located well to the right.

Wind on the night of 16-17 June varied from 17 to 22 mph and the pattern is clear (fig. 3). It varied from 13 to 18 mph on 23-24 July and the pattern appeared. On 1-2 August the wind varied from 2 to 8 mph, but the temperature fell 14°F; the pattern is obscured by fluctuations between the peaks. Thus, if the effect of wind be removed, it is seen that temperature plays a major role in determining flight activity. The fact that most Trichoptera species fly *en masse* at night and not during the day when temperatures are higher, suggests an inhibiting effect of either or both of temperature or light. Wind can only make it difficult, or impossible, for the insects to fly, and thus to come to the trap, no matter how much they may be encouraged to fly by high temperature. The pattern will remain clear but numbers will be reduced. Thus wind and

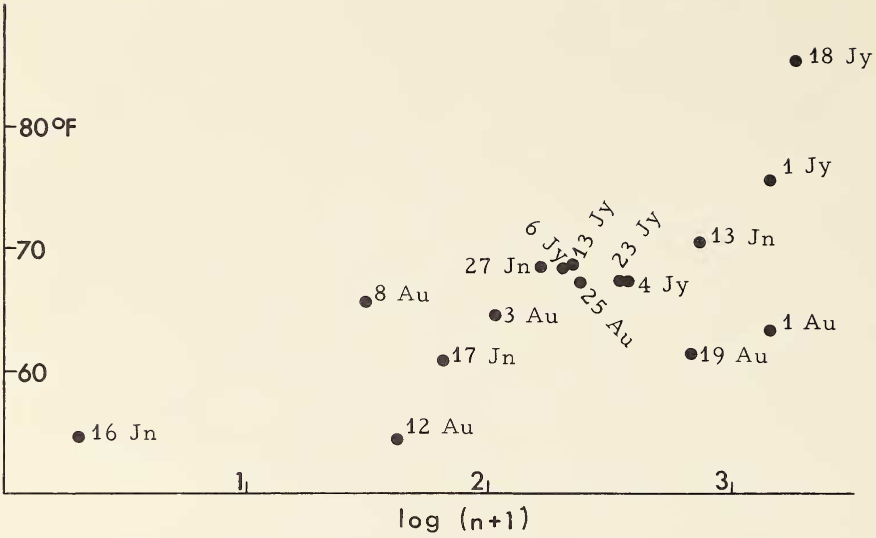

Figure 5 - Mean night (plus sunset & sunrise periods) temperature plotted against mean log (n + 1) of the hourly catch of Trichoptera.

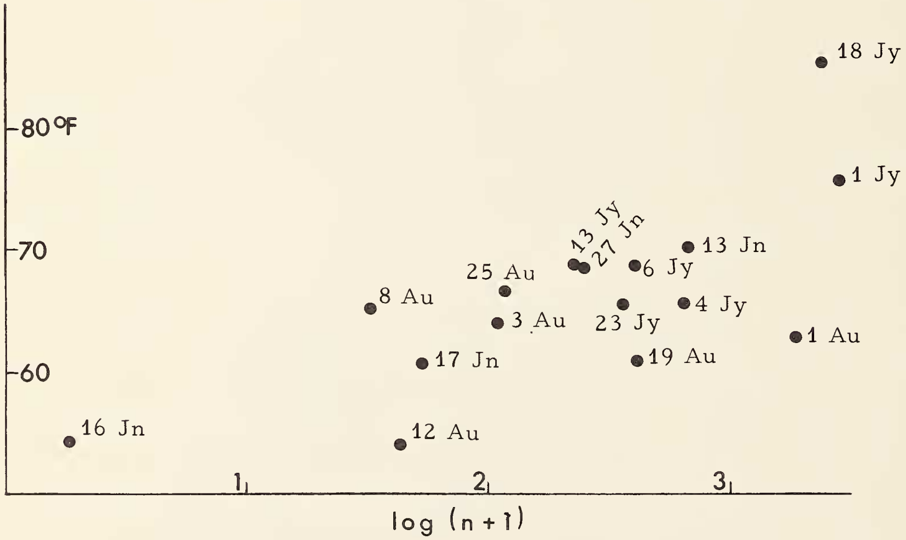

Figure 6 - Mean night (inter-peak) temperature plotted against the mean log (n + 1) of the hourly catch of Trichoptera.

temperature seem to be major factors in determining the overall catch for any one night. But the peaks, barring such exceptional circumstances as occurred on the night of 18-19 July, will remain detectable.

The periods between the peaks - To determine more precisely the effects of environmental factors the peak period data must be omitted from consideration, and the inter-peak periods examined more closely. The periods involved here are numbers 3 to 7, 3 to 8, or 3 to 9, depending on the time of sunrise.

Saturation deficit is not considered as it fluctuates from one hour to the next, with no apparent correlation with Trichoptera numbers. Figs. 6 and 7 illustrate mean log (n + 1) plotted against mean temperature and mean wind speed, for the appropriate sets of periods on collection nights. Fig. 6 shows a strong correlation of temperature with mean log (n + 1). Wind speed (fig. 7) shows some negative correlation as expected, but this is obscured since wind is secondary to temperature. Figs. 6, 7, and 8 collectively demonstrate the role of wind in disrupting the effect of temperature on the flying population. Fig. 8 gives mean log (n + 1) plotted against mean temperature times mean wind speed. It will be seen that the distribution of nights is similar to that of fig. 7; as temperature is also involved, the vertical spread in fig. 8 is slightly greater than in fig. 7. In fig. 6, showing mean log (n + 1) against mean temperature, the distribution is entirely different, and the correlation is much improved, and positive. This is further evidence of the overriding effect of temperature and the subsidiary disrupting effect of wind on flight of Trichoptera in the time between the peaks.

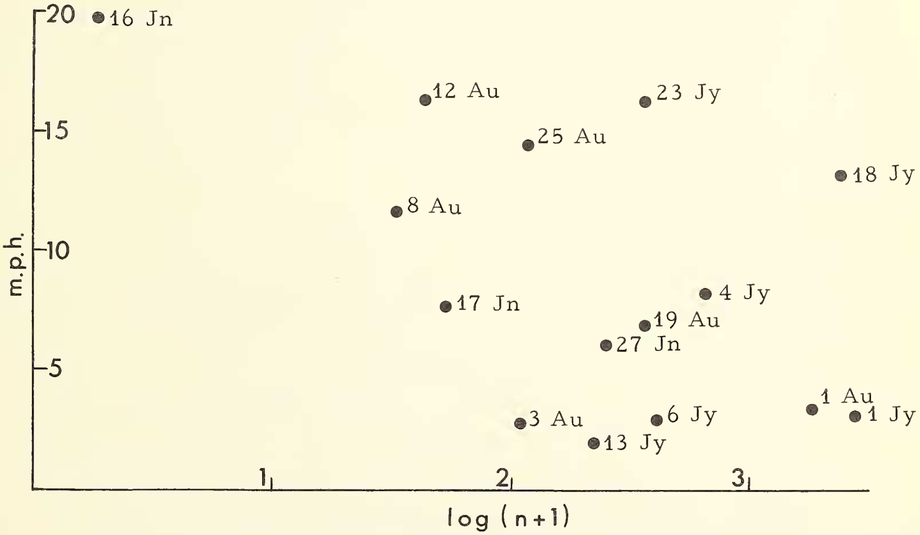

Figure 7 - Mean wind speed against mean log (n + 1) of inter-peak catch of Trichoptera.

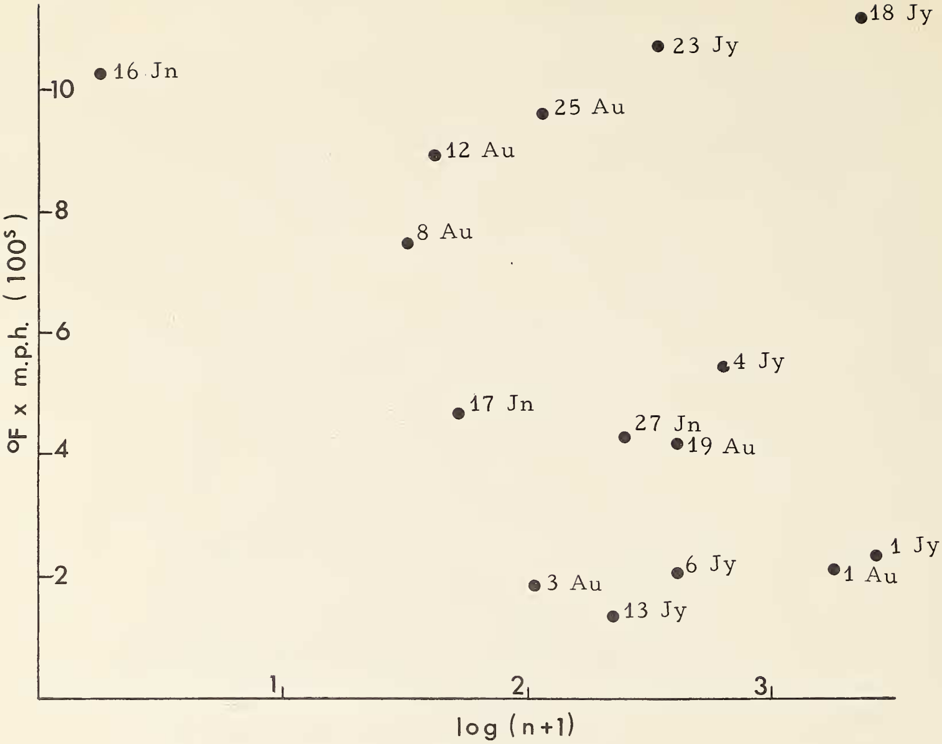

Figure 8 - Mean temperature X mean wind speed against mean log (n + 1) of inter-peak catch of Trichoptera.

Fig. 9 presents log (n + 1) plotted against temperature for each separate period, as limited in this section, for all catch nights. Again a definite correlation is seen, in more detail. The crosses represent the 5 catches from the night of 18-19 July and it will be observed that periods 3, 4, and 5, before the wind dropped, show low catches relative to the rest of the scatter.

In a statistical analysis of the data from inter-peak periods, the method of multiple correlation as set out in detail by Croxton & Cowden (1955) was used. Values of log (n + 1) are designated in the following as X_1; of temperature, X_2; of wind speed, X_3. Details of the calculations are omitted, suffice it to summarize the results, X_1 being the dependent variable:

Using one independent variable: X_2 or X_3

Total variation of X_1,	Σx_1^2	= 69.7634
Variation explained by use of X_2 only		= 32.4282
Standard error of estimate		= 0.6789
Coefficient of correlation,	r_{12}	= +0.6817

Thus variation in temperature serves to explain 68% of the variation in log (n + 1), or 68% of the changes in numbers are associated with changes in temperature.

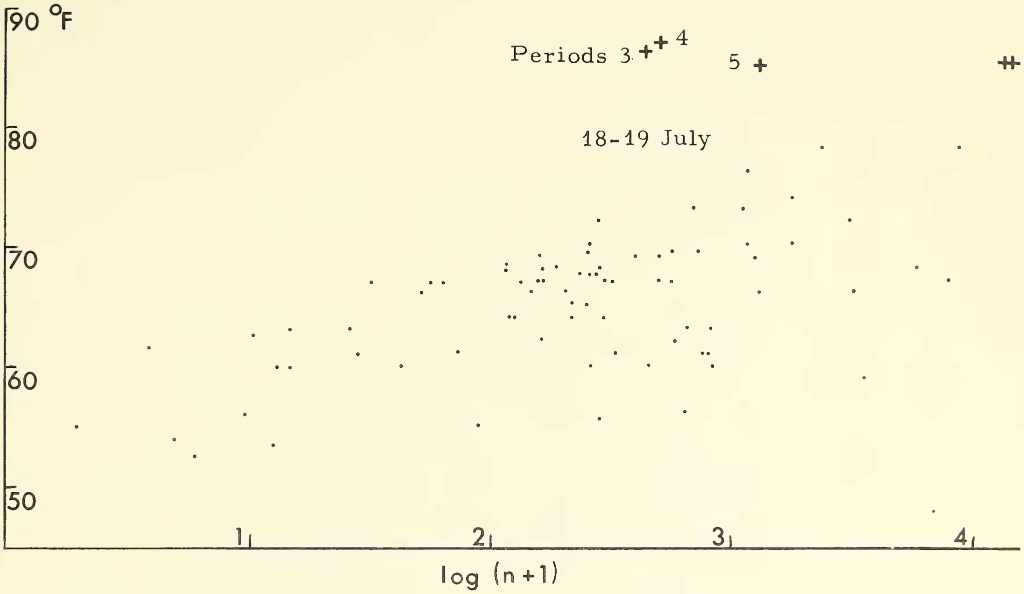

Figure 9 - Temperature against numbers of Trichoptera (as log (n + 1)) taken at an ultra-violet light trap at Ile Ste. Hélène, Montreal, summer 1964. Each 1 hour inter-peak period for all catch nights plotted separately.

Variation explained by use of X_3 only = 14.3372
Standard error of estimate = 0.8272
Coefficient of correlation = -0.4533

Thus variation in wind, serves to explain 45% of the variation of log (n + 1); i.e. 45% of the changes in log (n + 1) are associated with changes in wind speed.

Using two independent variables: X_2 and X_3

Total variation, x_1^2 = 69.7634
Explained variation, $x_c^2.23$ = 39.6811
Coefficient of correlation, $R_{1.23}$ = +0.7541

Thus temperature and wind speed together account for 75% of the variation of log (n + 1); i.e. 75% of the changes in log (n + 1) are associated with changes in temperature, wind speed, or both.

As the combined effect of these two factors on numbers of insects taken is to the extent of 75%, the interaction of temperature and wind may be assumed to be 38% (i.e. 45- (75-68) = 38). The remaining 25% of variation may be attributed to saturation deficit and other unmeasured and unrecognized factors. An application of the F test for the reliability of $R_{1.23}$ shows this to be clearly significant, that is, the correlation between X_1, and $X_{2 \& 3}$ appears to be very good.

The pattern at the species level- For each species the graphed pattern of only one night is used as the species patterns follow the total numbers pattern closely. The night chosen for each species was that which showed the pattern most clearly. Varying seasonal occurrence prevented the same night being used for all species, but only two nights were needed: 13-14 June and 25-26 August. Species and night are given in fig. 10. It will be seen in these graphs that all seven species tend to follow the pattern, with differences, of course, but these are minor.

Included in fig. 10 are 2 additional graphs, for *H. recurvata* and *C. speciosa* . They are both for the night of 18-19 June on which the speed suddenly decreased. In these two figures an evening peak is discernible, especially in *H. recurvata* . The overall depression of the first half of the night shows, but the species numbers rose to a peak, then fell away; the wind dropped and the numbers recovered to the assumed 'normal' for that night. On this night *Athripsodes cancellatus* also showed a peak, but not so well. The interesting point here is, that it was the three *large* species (body length > 4 mm) which produced discernible evening peaks of flight activity despite the high wind. Three other species, *Psychomyia flavida* , *Protoptila maculata* , and *Hydroptila spatulata*, showed no evidence of a peak at all: they are all micro-Trichoptera. Thus size is seen to be of importance to a species in maintaining the pattern of night time activity, if winds are high and fluctuating. This diversity due to size may well be another factor in the 25% variation in log (n + 1) remaining to be explained.

In fig. 4 are graphs of the patterns using mean values of log (n + 1). Allowance should be made for sunrise shift.

Sex Ratios

Sex ratios were examined to determine if the sexes were active at different times. In all seven species considered in detail, at least fifty per cent of the total numbers of each night arrived by period three. In most cases the ratio is about 50 throughout the night.

It seems safe to conclude that the pattern of total numbers of Trichoptera taken at light is due neither to any one sex of any one or more species, nor to any species as a whole.

Ten Minute Catches — Total Numbers

Fig. 11 shows patterns for individual nights using log (n + 1) values, and fig. 12 shows the average pattern for the summer, using mean values of log (n + 1).

The points to observe are as follows. For the first six periods there were no catches or, at most, small numbers: occasionally catches in periods 4 to 6 were substantial. The peak of flight activity generally occurred in catch period 7 but sometimes in period 6, 8, or even 9.

From figs. 11 and 12 it will be seen that the peak follows immediately after civil twilight. Fig. 13 shows that a sharp change in rate of decline of light intensity occurs at civil twilight.

The curve of activity generally starts to rise prior to civil twilight, indicating a response either to low, or a lowering of, light intensity. However, the sudden upsurge to the peak seems to be associated with the sudden change in rate of decline of light at civil twilight. Harker (1961)

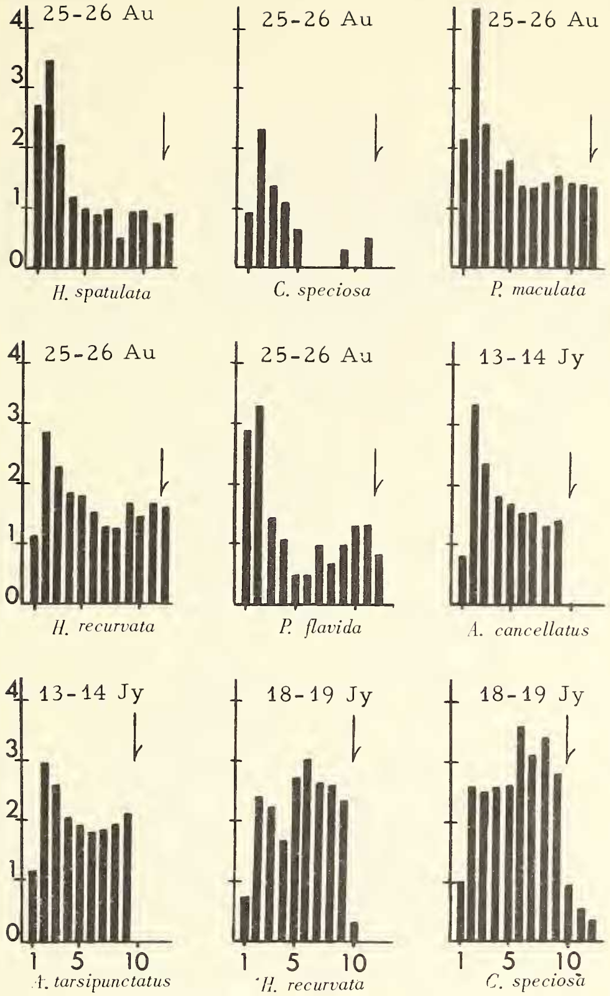

Figure 10 - Pattern of arrival on selected nights of seven species of Trichoptera at a UV light trap at Ile Ste. Hélène, Montreal, summer 1964. Two additional graphs are included for reasons given in the text. Abscissae in 1 hr periods, ordinates numbers as log (n + 1). Sunset coincident with the first period mid-point. Sunrise indicated by arrows.

points out that "..., it is rare for activity to occur as an immediate reaction to change in light intensity". It could be, therefore, that the peak is a delayed reaction to the light values of earlier periods, which are themselves vastly lower than normal daytime values. Nielsen's (1963) summary of the situation in poikilotherms: "The releasing factor may be a certain low level of illumination, or it might be a certain rate of change of intensity or a combination of both" seems appropriate to the uncertainty concerning the role of natural light in producing the peaks in Trichoptera. One further possibility is that the change in the rate of decline of light intensity induces an immediate increase in flight activity.

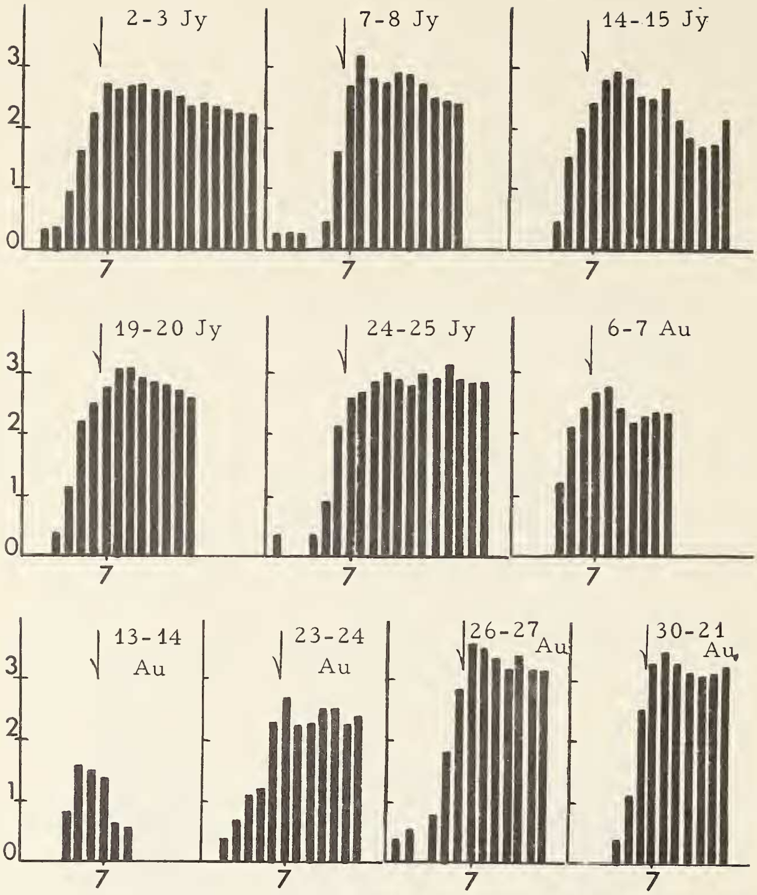

Figure 11 - Total number of Trichoptera taken at a UV light trap at Ile Ste. Hélène, Montreal, summer 1964, for each night on which 10 min catch periods were used. Ordinates in log (n + 1), abscissae in 10 minute periods, log values plotted at the period mid-points. Civil twilight indicated by the arrows.

DISCUSSION

Previous Studies of Nocturnal Activity Patterns in Trichoptera

Light trap studies of the nocturnal flight activity rhythms of insects of immediate interest, are those by Williams (1935 and others), Stage & Chamberlin (1945), Southwood (1960), Corbet and Tjønneland (1955), and Brindle (1957 a, b, and 1958). Most papers mention Trichoptera in passing, if at all. Trichoptera have been studied seasonally (Crichton 1960, Marshall 1939), rather than hourly, as here; such studies are consequently of little interest in the present context. It is unfortunate that there appear to have been no studies of Trichoptera using non-attractive traps, other than that of Lewis & Taylor (1965).

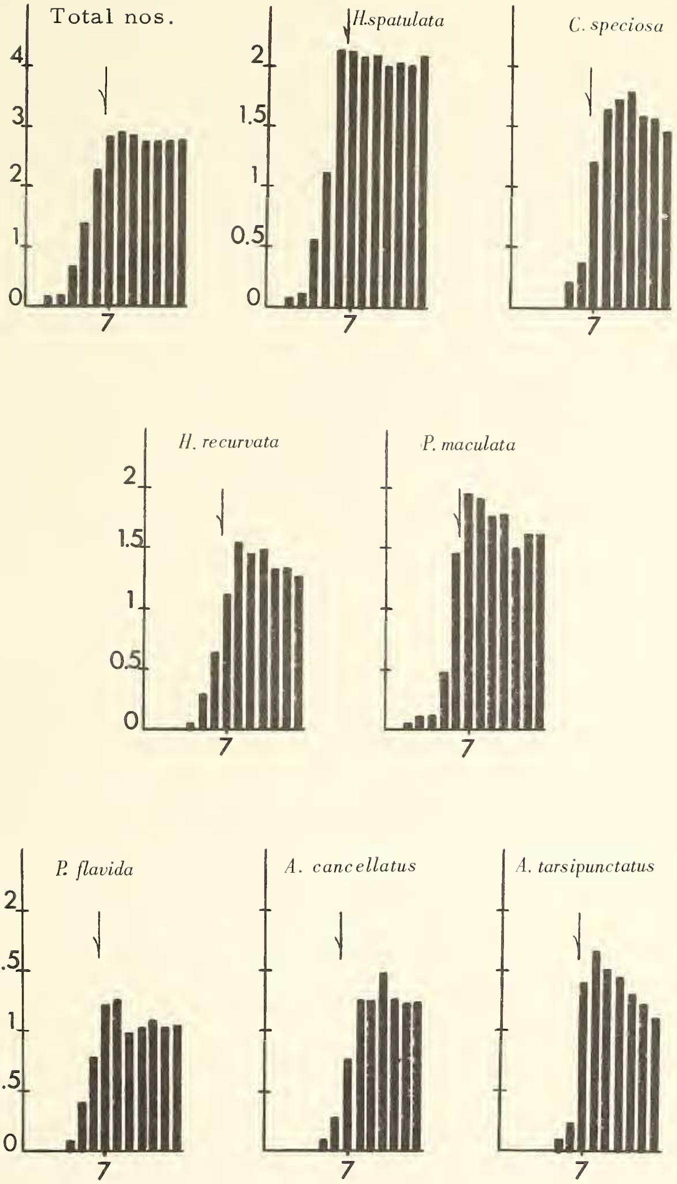

Figure 12 - Means of numbers of Trichoptera taken per 10 min period at an ultra-violet light trap at Ile Ste. Hélène, Montreal, for those equivalent periods of each night on which trapping was carried out, summer 1964. Abscissae in 10 min periods, ordinates in log (n + 1) with values plotted at period mid-points. The arrows mark civil twilight.

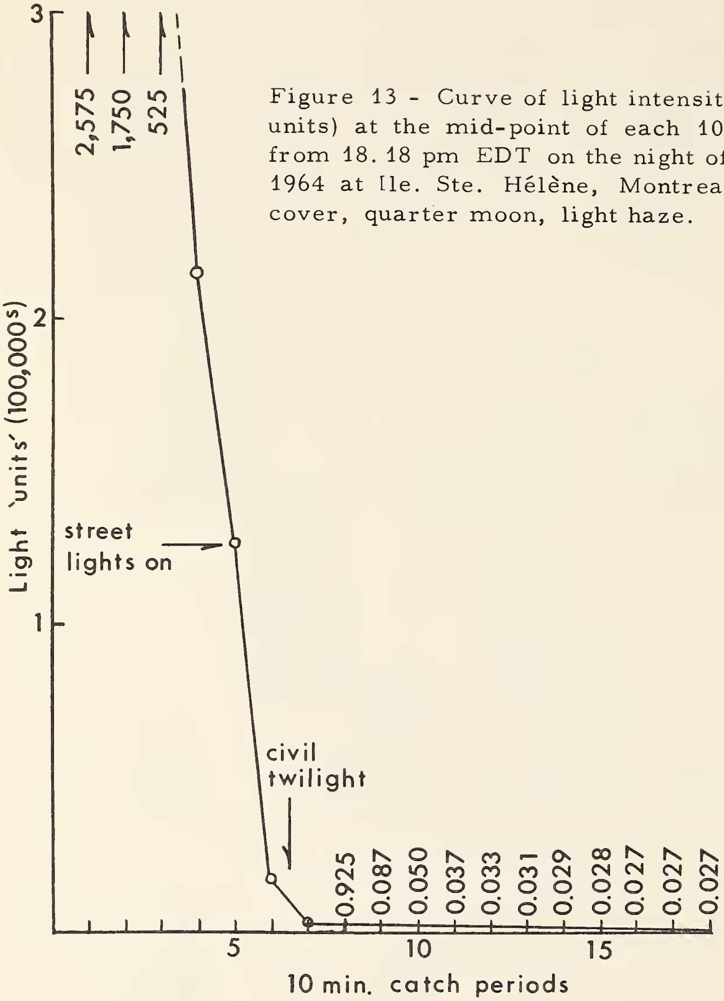

Figure 13 - Curve of light intensity (arbitrary units) at the mid-point of each 10 min period from 18. 18 pm EDT on the night of 14-15 July 1964 at Ile. Ste. Hélène, Montreal. No cloud cover, quarter moon, light haze.

The Pattern at Montreal

The pattern found in this study has the following characteristics: bimodal, the evening peak relatively much more pronounced than the morning peak; the pattern of numbers in periods exclusive of the peaks forms a gradually decreasing slope from the evening peak till the slight rise to the morning peak; the interpeak slope may be punctuated by fluctuations of varying degrees, dependent on meteorological factors; the morning peak is terminated by an abrupt drop-off in numbers to zero, or almost zero. Referring to Corbet & Tjønneland's (1955) classification of relative development of the two peaks in East African Trichoptera, the present 7 species seem to fit their class 2 well; "Both peaks discernible, dusk peak far more pronounced".

Meteorological Factors and the Pattern

The day-to-day effects of temperature and wind were dealt with here only superficially, for two reasons: 1). The paucity of data did not warrant any emulation of, for example, Williams' work on Lepidoptera (1961) and Simuliidae (1962) in this respect and, 2). this was not the purpose of the study. The analysis here was done simply as a step towards examination of the inter-peak fluctuations, and to aid in determining the role of light. The gross effect of temperature and wind on magnitude of the total catch on any one night has been demonstrated and Williams (1961) says that "The activity of insects on any one night is very largely determined by temperature and wind, . . . ". Brindle (1957a) mentions the effect of wind on two night's catches. Each night the wind was from a different quarter: once from a river, once from a reservoir. The species composition differed remarkably on these nights and corresponded with the fauna of the source from which the wind blew. One species was common to both nights however, but not to both habitats, ". . . a strong flyer" as Brindle says and, being a species of *Phryganea*, it is a 'large' trichopteran. This, again, agrees with the evidence from the night of 18-19 July, for the differential effect of wind depending on insect size. Brindle also examines the effect of temperature and relative humidity and finds higher temperatures, associated with lower relative humidity, better for larger catches. It is uncertain how he regards relative humidity, but certainly there is agreement on temperature effects. My determination of temperature and wind as prime factors in determining the total catch of any one night is in general agreement with the few papers which deal specifically with Trichoptera activity patterns and weather, and with Williams' (1961) statement.

The Role of Light Intensity

The role of natural light in producing the peaks in numbers taken at dusk and dawn at artificial light, has previously been examined only by Corbet & Tjønneland (1955). They concluded that flight is inhibited by light above a certain intensity. At intensities below this light is conducive to mass flight activity; at still lower intensities flight activity dwindles but does not cease entirely. They speculate that activity is positively correlated with light intensity, up to the inhibiting value, but do not explain why flight occurs when it is almost dark, as between the peak periods.

It has been shown here that the evening peak was preceded by a sharp upsurge from zero, just prior to civil twilight. The sharp drop-off after the morning peak seems to mirror the sharp rise before the evening peak. Detailed examination of the morning peak may be expected to show that the sudden drop occurs very close to but after morning civil twilight, as found by Corbet & Tjønneland in Africa. One possible explanation for the relative insignificance of the morning peak may be found in the fact that light is increasing, rather than decreasing. I have suggested that the evening peak is triggered by a certain light value, but that all that is needed for night activity, is light lower than a certain intensity (see fig. 13). If this is so, the increase in light in the morning prior to attainment of the crucial light intensity, should have little effect on the numbers taken. Then, when the critical intensity occurs, little time will be available for a peak to develop as the conditions of full daylight which follow inhibit flight.

Meteorological Factors and the Inter-Peak Periods

A pattern of steadily but gradually decreasing numbers between the evening and morning peaks appears to be usual at Montreal and resembles that described by Corbet & Tjønneland (1955). Meteorological factors play a vital role in determining the level of the pattern provided their action is steady or non-violent throughout the night. However, the inter-peak pattern will reflect any sudden changes in meteorological factors.

Corbet and Tjønneland ran their trap on nights in which the meteorological factors varied little from night to night, or within nights. Thus they had no opportunity to determine the effect of fluctuations on their catches. They used 10 min catches throughout the night and those of their species which showed patterns similar to the one here, but much more clearly, showed a certain amount of fluctuation between the peaks which is not directly attributable to any factors considered here, and can probably be labelled intrinsic. But though they experienced only light breezes they did demonstrate the differential effect of wind on species of various sizes; they did not relate wind directly with pattern fluctuations, but appear to have done so indirectly. Thus part of the apparently intrinsic variation may have been due to light wind and small species.

Natural Affinities of the Pattern

To determine the actual daily flight activity pattern of Trichoptera, some trapping method is required which collects independently of any response on the part of the insects (e.g. Lewis & Taylor 1965). It seems reasonable to suppose that, in species showing a bimodal activity pattern such as were worked with here, the pattern *between* the tips of the peaks is a reflection of the natural pattern. The gradual decrease from the usually much larger evening peak, towards the morning peak is ignored for the present. The point is that a certain basic level of activity appears to be demonstrated between the peaks. Whether this is the same level as the daytime flight activity level, or higher or lower, cannot be said. But daytime flight is not uncommon in Trichoptera (Brindle 1957a, Peterson 1952, Lewis & Taylor 1965). Daytime flight, especially in late afternoon was frequently observed in several species at Ile Ste. Helene. Swarming activity, especially by *H. recurvata*, was common. So it may be, in some species, that the nighttime level may be the low point of the 24 hour period, and the peaks the result of inducement to still greater activity. But most species generally only *appeared* flying after sunset. Some lack of response to the mercury vapour light may explain part of the abrupt rise and fall in evening and morning, but as the change from twilight to full sunlight, is gradual, so also should the decrease in attractiveness of the light be gradual, which it is not. But from just what level of a flying population the evening rise, for example, is abrupt, cannot be deduced here. Considering the day activity of some species, the abrupt rise may be explained by the light gradually becoming effective when the flying population is already at a high level. However, the peaks, as such, above this level, can only be regarded as natural phenomena in themselves, due to the gradual decrease after the evening peak and the slight rise preceeding the morning peak.

Another point which may support the 'natural' peak is the spectral quality of the light source (see table 1 p. 220). Emitting largely in the short wavelength end of the spectrum, the bulb should appear in daytime as a discrete source of stronger radiation of these attractive wavelengths. The smaller numbers of insects taken in the trap in daytime may be attributed in part to competition of daylight with the trap light source and in part to less activity. In a way, therefore, the use of a mercury vapour light source may actually provide a preliminary guide as to whether or not the pattern is natural. It is proposed that, in its essential features, it is, for those species which exhibit it.

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